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Abstract

External male genitalia of the three pitheciine genera appear to be uniquely designed for direct delivery of sperm into the uterus. Described is the gross anatomy of five of the six species of *Pithecia* and the two each of *Cacajao* and *Chiropotes*. The shaft in pitheciines is evenly tapered to tip, subtriangular in cross section, curved upward in some, downward in others with cant to right or left, labile glans undifferentiated from shaft, meatus bordered by erectile lappets. Penile shape, curvatures and glans accessories facilitate coupling of the meatus with the uterine cervix and possible direct transfer of sperm into the uterus. The baculum of each species of *Pithecia* is distinctive, the penile spines minute. Remaining pitheciines lack a baculum but have large, hooked penile spines.

Hypertrophied penile spines of *Chiropotes* and *Cacajao* may lock into the vagina after intromission and/or open a passage through ejaculates of previous multimale copulations. The little that is known of pitheciine sexual and social behavior is recorded.

Introduction

External male genitalia of pitheciines (Pitheciinae, Cebidae) are among the least studied of primate reproductive organs. Known heretofore are descriptions of the external genitalia of one specimen each of a *Pithecia pithecia* and a *Cacajao rubicundus* by Hill (1958, p. 645, 1960, pp. 184, 226, 227 with figure) and of *Cacajao calvus* by Fontaine and Du Mond (1977, pp. 201, 203).

The present account describes the male external genitalia of all but one (*Pithecia albicans*) of the nine known species of the three genera of Pitheciinae, and the system that seems to have evolved for direct sperm transfer from penis into uterus. Notes on social organizations are included. Most recent taxonomic revisions of the genera are by Hershkovitz. They are those of bearded sakis, genus *Chiropotes* (1985), uacaries, genus *Cacajao* (1987a), and sakis, genus *Pithecia* (1987b). Genitalia and sexual behavior were not considered in these revisions.

Material

Thirty-eight male external genitalia are described (table 1). Of these, 12 are entire, that is, with intact penis, scrotum, and surrounding integument, fixed in formalin, and preserved in alcohol. The remaining 26 are terminal ends of penes excised from dry museum skins, hydrated, cleared in 2–4% potassium hydroxide (KOH), and stained with alizarin to reveal the baculum, if any.

The cleared penes are gelatinous in texture, tumescent as in erection, but often bloated. Adornments such as lappets surrounding the urinary meatus are usually swollen as in erection.

FURROWS—The integument of nearly all penes examined is evenly furrowed all around. In contrast, penile skin of the live or freshly killed animal is loose, wrinkled, or folded without suggestion of furrows or corrugations or indication of tendency toward their formation. Perhaps the differential responses of skin and underlying tissues to fixation and/or chemical clearing combine to produce fur-

rows. In a casual inspection, furrows were noted in similarly prepared and preserved penes of *Ateles, Cebus,* and *Macaca.*

Measurements

Intact and extended penes were measured from base at scrotal margin to tip of glans. Full length of a completely erect penis in the live animal is conjectural but may be approximated by those of some cleared specimens. However, most detached, cleared penes, including glandes, used in this study are less than half of full length. Their measurements are included nevertheless in the descriptions. Greatest length of each baculum is given.

Body size dimensions given for species and specimens examined serve as bases for estimates of proportional size of external genitalia. The dimensions used are means and extremes of combined head and body length (HB), greatest skull length (GSL), and weight in grams (W). Measurements for the species are from Hershkovitz (1985, 1987a,b). Those of individual animals are from the original data sheets.

Abbreviations

AMNH	American Museum of Natural History, New York
FMNH	Field Museum of Natural History, Chicago
MPEG	Museu Paraense Emilio Goeldi, Belém
RNHMS	Royal Natural History Museum, Stockholm

Pitheciine Characters

Male external genitalia of the three genera of Pitheciinae exhibit increasing specialization from those of *Pithecia* to those of *Cacajao* and *Chiropotes.* Shared characters include scrotum sessile, parapenial, skin glandular with thin covering of pale hairs; testes subequal in size, descended in young and adults, retractable in both; baculum small, or absent in *Pithecia,* absent in *Chiropotes* and *Cacajao*; penis tapered to tip, subtriangular in cross section and more or less canted to either side of midline; glans undifferentiated from shaft by nonexpansion or nonconstriction at neck; urinary meatus a vertical or medioventral slit, its borders swollen with an extensile or erectile lappet distally, another proximally; penile spines minute in *Pithecia,* large in *Cacajao* and *Chiropotes.*

Body size of each of the five species of Pithecia is approximately equal. Size of each of the two species of *Cacajao* average larger, and that of each of the two species of *Chiropotes* is largest.

Generic Characters

Pithecia Desmarest (Sakis) (figs. 1, 2; tables 1, 2)

Genitalia of 4 available of the 5 known species appear to be similar. Scrotal sac is pigmented, skin glandular, the glands not always visible to the unaided eye, testes descended, penis arising from anterior scrotal margin curved downward or posteriad, longitudinal axis of shaft convex or concave dorsally, concave or convex ventrally, cross section subtriangular with apex dorsal, shaft canted right or left, spines extremely minute. Baculum present in 2 of 4 cleared penes of *P. pithecia,* 1 of 2 *P. monachus,* the single *P. aequatorialis,* and absent in the single *P. irrorata* (table 2).

Chiropotes Lesson (Bearded Sakis) (figs. 3, 4; tables 1, 2)

Scrotum almost entirely unpigmented, skin visibly glandular; testes descended but presumed retractable in all 8 available specimens including those of 5 young; longitudinal penile axis of *Chiropotes satanas* usually concave dorsally, convex ventrally as in *Cacajao calvus,* subtriangular in cross section with apex dorsal; penile shaft curved or canted left or right touching scrotum; shaft of *C. albinasus* with convexity and apex of cross section dorsal as in *Pithecia pithecia*; baculum absent in both species.

Cacajao Lesson (Uacaries) (figs. 5, 6; tables 1, 2)

The single available scrotum of a mature *C. calvus calvus* is entirely pigmented, the skin without macroscopically detectable glands; penis projected

TABLE 1. Male external genitalia described in this study. Intact genitalia include scrotum, penis, and part of perineum.

Taxon	Intact	Cleared penis only	Baculum (mm)
Pithecia pithecia	2	4	1.5; 3.0
Pithecia monachus	2	2	2.5
Pithecia irroratus	—	1	—
Pithecia aequatorialis	—	1	1.5
Chiropotes albinasus	—	1	—
Chiropotes satanas	8	10	—
Cacajao calvus	—	3	—
Cacajao melanocephalus	—	4*	—

* Three decomposed.

from inguinal border of scrotum curved upward or anteriad, with a 30° twist or cant to right; longitudinal axis of shaft variable, cross section subtriangular with apex ventral; curvature of two cleared partial penes of *C. calvus* equivocal; penis and prepuce invested with large, grappling spines; baculum absent in cleared penes, not palpable in untreated specimens.

Cleared shaft of *Cacajao melanocephalus* (fig. 5) is convex dorsally, concave ventrally as in *Pithecia*, subtriangular in cross section, apex dorsal; spines larger and thicker than those of *C. calvus*, but this may be individually variable; baculum absent.

Species Descriptions

Noteworthy interspecific differences among adult genitalia of congeneric species, bacula excepted, are not apparent. Because of the fragmentary nature of most of the cleared penes used to increase sample size, the description of parts of one specimen may be applied to missing parts of other specimens of the same species. Body size dimensions are given under each species heading; measurements of individual animals follow their registry number.

Pithecia pithecia Linnaeus (figs. 1a,b)

SIZE—HB = 363(330–395)9; GSL = 80.6(77.4–82.7)16; W = 1,740(1,380–1,866)9.

SPECIMENS—Six, including two intact external genitalia and four partial penes detached from dry museum skins, cleared, stained, and preserved in glycerine.

FMNH 95504 (HB = 348; GSL = 79.4)—Scrotum pear-shaped, greatest transverse diameter about 21 mm, wrinkled skin pigmented except the broadly distributed unpigmented or mottled ovate skin glands each with a triad of long brown hairs projecting from a minute pore; penis, issuing from anterior scrotal margin, mottled brownish except unpigmented borders of meatus; longitudinal axis of shaft slightly convex dorsally, concave ventrally, inclined or canted left; rounded glans undifferentiated from shaft but slightly wider on ventral than dorsal surface; meatus a 3-mm medioventral slit, its expanded ventral border with swollen triangular lappet, dorsal border with conical lappet, each lateral border with paired lappets; minute spines of shaft or glans not detectable macroscopically; baculum if present not palpable.

FMNH 95505 (HB = 349; GSL 79.6) (figs. 1a,b)—Scrotum more or less pear-shaped, greatest trans-

TABLE 2. Pitheciine penile forms of shaft (not all features completely determinable in some specimens).

Taxon	*N*	Lengthwise dorsal surface		Apex		Cant	
		Convex	Concave	Dorsal	Ventral	Left	Right
Pithecia pithecia	6	4	—	2	—	3	—
Pithecia monachus	4	2	1	1	—	—	3
Pithecia irrorata	1	1	—	1	—	1	—
Pithecia aequatorialis	1	—	1	1	—	1	—
Chiropotes albinasus	1	1	—	1	—	1	—
Chiropotes satanas	18	1*; 3†	8	8	—	4	9
Cacajao calvus	3	1*	1	—	3	—	3
Cacajao melanocephalus	4	1	—	1	—	1	—
Totals	38	14	11	15	3	11	15

* Glans twisted.
† Juvenals.

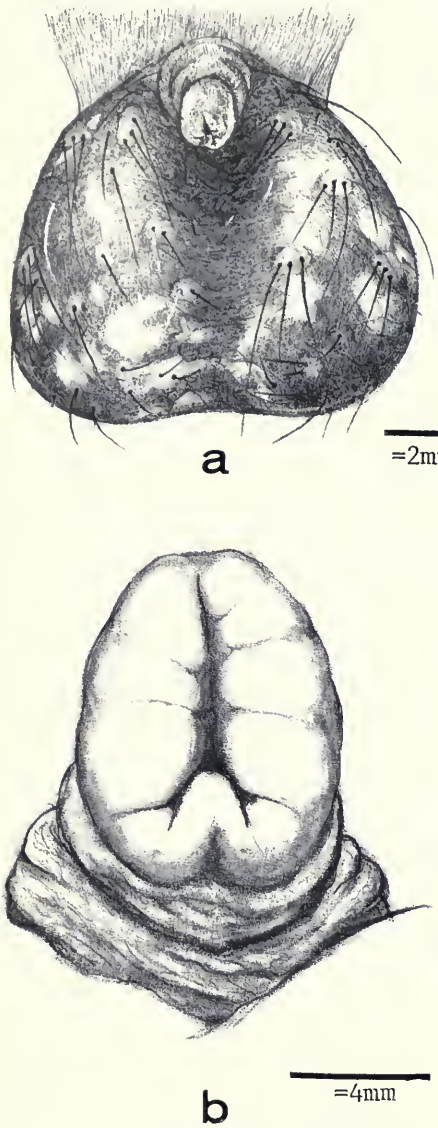


FIG. 1. *Pithecia pithecia,* external genitalia; **a,** intact, anteroventral aspect (FMNH 95505); **b,** glans of same, meatal aspect.

verse diameter about 19 mm, skin less glandular than that of preceding; completely extruded penis tapered, particolored, length about 20 mm, cant left, ventral raphe continued as frenulum at base of glans; shaft with dorsal surface narrower than ventral; meatus as in preceding but with ventral lappet extruded, dorsal lappet receded; spines not evident macroscopically; baculum if present not palpable.

FMNH **93251 (HB = 375; GSL = 78.7) (fig. 2c)**—Cleared unpigmented glans with fully developed tenpin-shaped baculum imbedded above meatus, its base subtriangular, greatest length, ca. 1.5 mm.

FMNH **93232 (HB = 360; GSL = 81.6)**—Cleared unpigmented penile fragment 5–6 mm long, surface furrowed, covered with nodular based minute spines; baculum in dorsal portion of tip 3 mm long, shape not clearly defined but seemingly like preceding; dorsum of shaft convex, cant left.

FMNH **50882**—Cleared unpigmented penile fragment about 17 mm long, shaft with dorsal surface convex, narrower than concave ventral surface; swollen horseshoe-shaped meatal borders as in preceding; shaft furrowed, with minute nodules each with spine; cant right; baculum absent.

FMNH **95507 (HB = 345; GSL = 76.7)**—Skin of cleared pigmented glans and fragment of furrowed shaft with minute nodules each with macroscopically invisible spines; dorsal surface convex, broader ventral surface concave, cant left; meatal borders swollen; baculum absent.

HILL (1958, 1960)—The description of external genitalia of an undetermined species of *Pithecia* does not mention a baculum. A subsequent report of the genitalia by Hill (1960, p. 184, fig. 34) describes the baculum of *Pithecia pithecia* as a "short (2.0 mm) pyramidal nodule, 1.75 mm in diameter at base, triangular in dorsal view, with a medial dorsal keel, and a pair of alai directed downwards and lateral enclosing a ventral concavity which encloses the fossa navicularis of the urethra." The accompanying figure is unlike adult bacula of *Pithecia pithecia* at hand, but the description in text suggests an incompletely developed or abnormal bone.

Pithecia monachus É. Geoffroy (figs. 2a,b)

SIZE—HB = 418(398–480)15; GSL = 87.2(82.1–92.7)40; W = 2,697(2,177–3,100)8.

SPECIMENS—Four, including two intact external genitalia and two penes detached from dry museum skins, reconstituted, cleared, stained, and preserved in glycerine.

FMNH **122796 (HB = 405; GSL = 83.0; W = 3,000)**—Pigmented scrotum with testes retracted, skin puckered, hairy cutaneous glands pronounced; furrowed shaft about 14 mm long, pigmented, slightly tapered, spines hardly evident un-

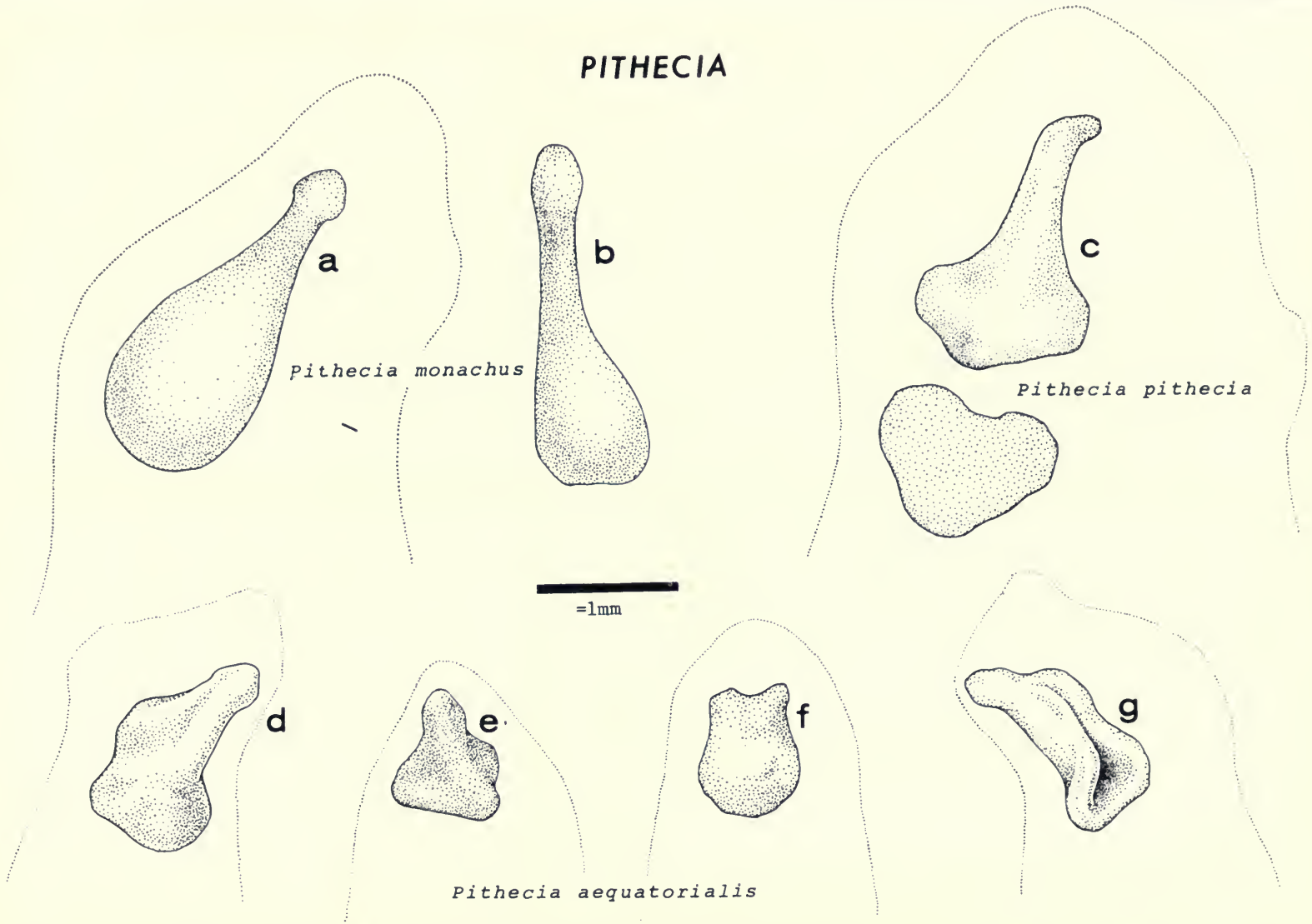


FIG. 2. *Pithecia*, bacula of three species; **a**, *P. monachus* (FMNH 87001), right side; **b**, same, dorsal surface; **c**, *P. pithecia* (FMNH 93251), right side and base; **d**, *P. aequatorialis* (FMNH 86995), right side; **e**, same, dorsal surface; **f**, same, ventral surface; **g**, same, left side.

der magnification, dorsum convex, cant right; baculum, if present, not palpable.

FMNH **122798 (HB = 409; GSL = 84.5; W = 2,500)**—Subadult, globular scrotum hardened, shrunken, its greatest diameter about 23 mm, puckered skin pigmented, triad of brown hair projecting from each glandular pore; shaft nearly entirely pigmented, dorsum slightly convex, cant right; meatus as in *P. pithecia,* ventral lappet extruded, dorsal lappet exposed; spines not evident macroscopically; baculum if present not palpable.

FMNH **25321 (GSL = 88.7)**—Cleared penis tapered, entire length about 15 mm; width at base 6 mm, of glans 4 mm, dorsal surface convex or concave, ventral surface concave or convex, shaft subtriangular in cross section with apex dorsal, cant right; ventral and dorsal lappets swollen; minute spines evident; baculum absent.

FMNH **87001 (HB = 434; GSL = 81.5) (figs. 2a,b)**—Cleared, partially disintegrated glans with dorsal and ventral lappets; spines if present not detectable macroscopically; club-shaped baculum near tip of dorsal lappet about 2.5 mm long (fig. 2a).

Pithecia irrorata Gray

SIZE—HB = 428(375–490)13; GSL = 89.4(86.1–94.3)19; W = 2,920(1).

SPECIMEN—Cleared penis, excised from dry museum skin, reconstituted, cleared, stained, and preserved in glycerine.

FMNH **98040 (HB = 419; GSL = 89.0)**—Penile fragment 10 mm long, furrowed, pigmented; shaft with longitudinal axis of dorsal surface convex, ventral concave, subtriangular in cross section with apex dorsal, cant left; dorsal and ventral lappets well defined; minute spines weakly defined; baculum absent.

Pithecia aequatorialis Hershkovitz (figs. 2d–g)

SIZE—HB = 417(394–440)4; GSL = 86.0(81.5–89.8)4.

SPECIMEN—Cleared penile fragment from dry museum skin, reconstituted, cleared, stained, and preserved in glycerine.

FMNH **86995 (HB = 394; GSL = 81.5) (fig. 2d)**—Pigmented penile fragment 13 mm long considerably distorted, flattened, nodular skin pigmented, indistinctly furrowed; shaft with dorsal surface concave, ventral convex, subtriangular in cross section with apex dorsal, cant left; spines if present not detectable; dorsal and ventral lappets hardly defined in distorted, partially disintegrated glans; baculum about 1.5 mm long, subglobular with lateral borders redoubled forming a longitudinal sulcus (figs. 2d–g).

Pithecia albicans Gray

SIZE—HB 465(404–560)10; GSL = 85.4(83.3–89.2)12.

SPECIMENS—None. Dixson (1987b, p. 52) gives 1.5 mm for baculum length of the single specimen examined.

Chiropotes albinasus I. Geoffroy (figs. 3a–c)

SIZE—HB = 431(390–470)8; GSL = 93(90.0–97.1)12; W = 2,487(2,200–2,720)7.

SPECIMEN—One partial penis removed from dry museum skin, cleared, stained, and preserved in glycerine.

MPEG **8151 (skin without data, skull missing)**—Longitudinal axis of shaft slightly convex dorsally, plane ventrally, the surface with median crest, cross section subtriangular with apex dorsal, cant left; spines large, their orientation in all directions appears normal but may be an artifact of preparation and preservation (figs. 3a–c); baculum absent; furrows not distinct.

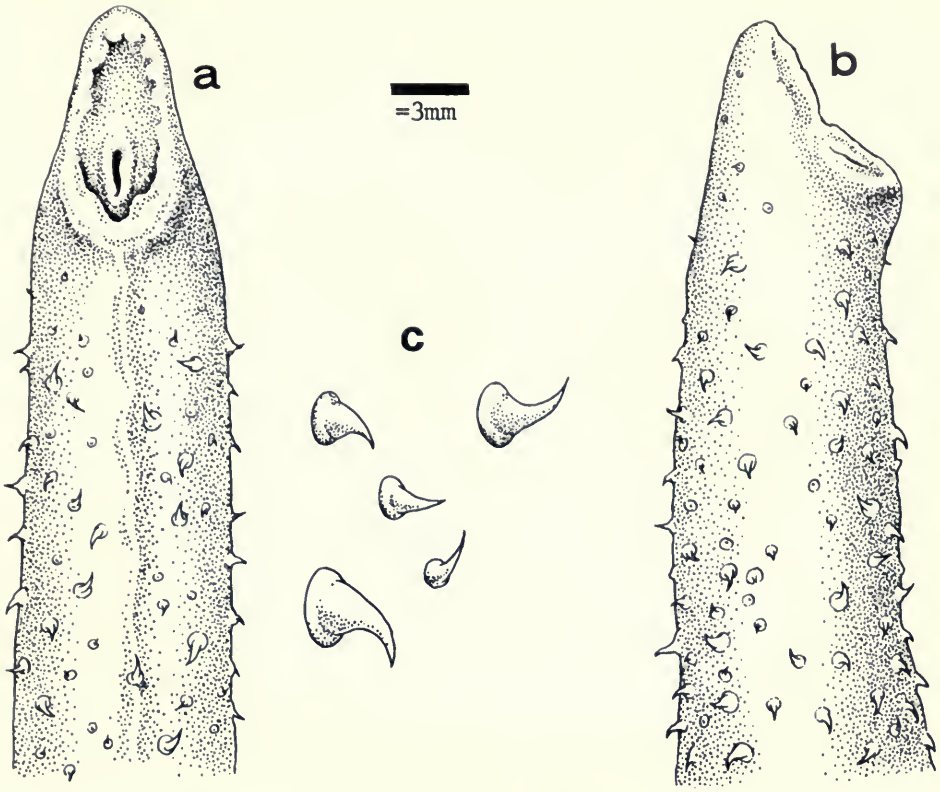
Chiropotes satanas Hoffmannsegg[1] (figs. 4a–d)

SIZES—*C. s. chiropotes*: HB = 423(370–507)20; GSL = 91.4(84.3–94.9)23; W = 2,904(2,200–4,000)20. *C. s. satanas*: HB = 382(335–424)15; GSL = 86.2(80.5–92.4)16. *C. s. satanas*: HB = 390, 440; W = 2,510, 3,000.

SPECIMENS—Eighteen, of which 8 are intact external genitalia fixed in formalin and preserved in alcohol, the organs hard, shrunken; 10 penes excised from dry museum skins, cleared, and preserved in glycerine.

FMNH **57691 (adult)**—Subovate scrotum infested with cuterebrid larvae, width 55 mm, skin unpigmented except dark brown triangular patch of anterodorsal section, thinly hirsute; scrotal and perineal skin crimped, puckered; penis partially

[1] The name *Chiropotes satanas utahicki* Hershkovitz (1985, p. 17) for Uta Hick (now Uta Ruempler) must take the feminine ending. It is herewith emended to *Chiropotes satanas utahickae.*



CHIROPOTES ALBINASUS

FIG. 3. *Chiropotes albinasus* (MPEG 8151; KOH preparation); **a**, ventral surface of shaft; **b**, same, right side; **c**, same, spines enlarged.

destroyed by parasites, completely sheathed, shaft with longitudinal axis of dorsal surface concave, of ventral convex, unfurrowed circumferentially; cross section subtriangular with apex dorsal, spines large, baculum absent.

FMNH 95786 (HB = 406; GSL = 93.5)—Diameter of scrotum about 55 mm, skin less puckered than that of preceding, dark brown triangular hirsute patch more extensive; greatest length of extended penis, 20 mm, exposed shaft tapered, furrowed, glans undifferentiated from shaft; shaft with longitudinal axis of dorsal surface deeply concave, ventral surface convex, cross section subtriangular, apex dorsal; penis sharply canted left, nearly touching scrotum; longitudinal slit of meatus about 3 mm, lateral borders swollen, ventral lappet small, dorsal lappet bulbous, protrusion about 3 mm; prepuce spiny; baculum absent.

FMNH 95512 (HB = 407; GSL = 91.8) (figs. 4a-d)—Scrotum ovate, wider than long, greatest diameter about 45 mm, skin unpigmented except eumelanin speckling of dorsal surface proximal to penis, skin puckered, wrinkled, thinly covered with triads of long blond hairs each issuing from a glandular pore; long dark guard hairs uniformly dispersed; anterodorsal surface of scrotum with triangular patch of dark brown hair, the skin speckled; scrotum divided by moderately deep sulcus anteriad to base of penis; perineum broad, smooth, unpigmented; penis projecting from midscrotum, length about 30 mm, basal half sheathed, exposed terminal half corrugate and furrowed, cant left, the shaft nearly touching scrotum, glans pointed upward; hooked spines prominent, the longest about 0.6 mm; longitudinal axis of dorsal surface of shaft concave, ventral convex, subtriangular in cross section with apex dorsal; baculum if present not palpable.

FMNH 57692 (juv.)—Scrotal halves spread, greatest transverse diameter about 45 mm, individual testis smaller than that of preceding specimen; length of preputial or sheathed portion of

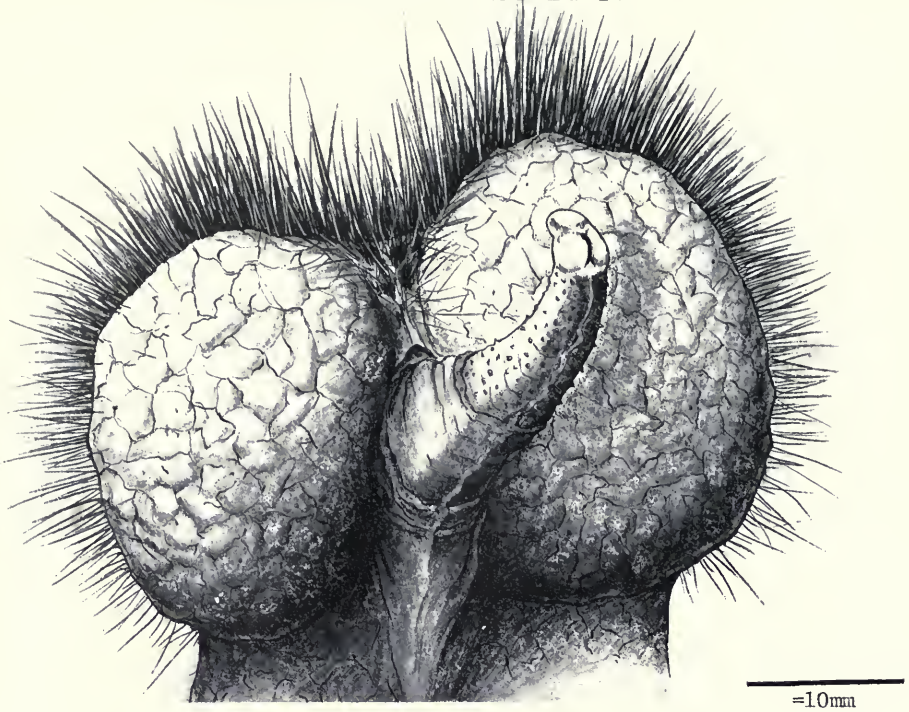


FIG. 4. *Chiropotes satanas*, external genitalia of mature male; **a,** intact, anteroventral aspect (FMNH 95512); **b,** distal portion of shaft (KOH preparation), right side (AMNH 518225); **c,** same, ventral surface; **d,** same, penile spine enlarged.

penis about 9 mm, curvature indeterminable but longitudinal axis of dorsal surface possibly convex; spines if present not evident, baculum not palpable.

FMNH **93256 (no individual measurements)**—Transverse diameter of scrotum 35 mm, unpigmented skin puckered, thinly covered with blond hair; penis emerging from lower anterior third of scrotum completely ensheathed within spinous prepuce, penile shape and curvature not precisely determinable.

FMNH **95348 (juv.)**—Greatest transverse scrotal width about 34 mm; length of sheathed shaft with small portion of glans visible about 18 mm; shaft with longitudinal axis of dorsal surface convex; spines not evident; baculum not palpable.

FMNH **57690 (juv.)**—Right testis missing; length of nearly entirely sheathed penis about 18 mm; dorsal curvature of shaft convex; spines not evident; baculum not palpable.

FMNH **57689 (juv.)**—Greatest transverse diameter of unpigmented scrotum 37 mm, testes small; length of sheathed portion of penis 7 mm; spines not evident, baculum not palpable.

MPEG **6936 (HB = 440; W = 3,000)**—Length of cleared penile fragment about 40 mm, base 10 mm, distal constriction 5 mm; long axis of dorsal and ventral surfaces plane, shaft tapered, furrowed, cross section subtriangular, apex dorsal, cant right; spines present; ventral meatal lappet enlarged, dorsal lappet smaller; baculum absent.

MPEG **6915 (HB = 430; GSL = 94.3)**—Length of cleared penile fragment 30 mm, base 12 mm; furrowed shaft with surface concave, ventral convex, subtriangular in cross section, apex dorsal, cant right, spines prominent, baculum absent.

MPEG **6921 (GSL = 90.2)**—Length of cleared penile fragment 30 mm, shaft furrowed, dorsal surface concave, ventral convex, subtriangular in cross section, apex dorsal; cant right; spines present, baculum absent.

MPEG **8848 (HB = 410; GSL = 87.9)**—Length of cleared penile fragment 25 mm, 11 mm wide at prepuce; dorsal surface of furrowed shaft convex, ventral slightly concave, cant right, spines present, baculum absent.

MPEG **6935 (HB = 428)**—Length of cleared section of furrowed penis 21 mm; dorsum of shaft concave, cant right; spines present, baculum absent.

MPEG **6933 (HB = 430)**—Length of cleared furrowed penile fragment 16 mm, strongly concave dorsally with apical crest; cant left; spines present; baculum absent.

MPEG **6914 (HB = 430; GSL = 91.3)**—Cleared terminal penile fragment, the furrowed basal border with spines; shaft with dorsal contour concave, ventral convex, subtriangular in cross section with apex dorsal; cant left; baculum absent.

AMNH **518225 (HB = 380; GSL = 89.2; W = 2,500)**—Length of cleared, slender, furrowed penis 20 mm long; shaft with dorsum concave, cant right, spines present, baculum absent (figs. 4b–d).

FMNH **57685 (HB = 260)**—Cleared fragment of glans with vestige of baculum, original no. 93, no original data, labeled identification questionable.

FMNH **57686 (original no. 108)**—Cleared fragment of glans without original data, baculum absent; labeled identification questionable.

Cacajao melanocephalus ouakary Spix (figs. 5a-d)

SIZE—HB = 414(310–500)17; GSL = 99.9(91.2–108.8)21.

SPECIMENS—Four penes excised from dry museum skins, cleared, stained for bone, and preserved in glycerine; three of them nearly entirely decomposed.

FMNH **78567 (HB = 415; GSL = 99.5) (figs. 5a-d)**—Length of cleared tapered penile fragment 42 mm, diameter at base 10 mm, distal diameter below meatus 5 mm; shaft with dorsal surface convex longitudinally, concave ventrally, cross section subtriangular, apex dorsal, cant left, the raphe keeled; entire organ thickly vested with mostly large grappler spines, some nearly 1 mm long, most directed forward (distad), others back, still others at right angle to longitudinal axis, the orientation appears normal but may be an artifact of preparation and preservation; meatus longitudinal with lips swollen, terminal lappet approximately as long as meatus, its tip pigmented; baculum absent.

FMNH **78562-3, 78566**—All without penis bones, remaining fragments were presumably like comparable parts of preceding.

Cacajao calvus I. Geoffroy (figs. 6a–e)

SIZES—HB = 456(380–560)14; GSL = 100.1(96.8–103.8)14. HB = 400; W = 3,450.

SPECIMENS—Three, including intact external genitalia of one fully mature *C. c. calvus* and two partial penes of *C. c.* (subspecies?) detached from dry museum skins, cleared, stained for bone, and preserved in glycerine.

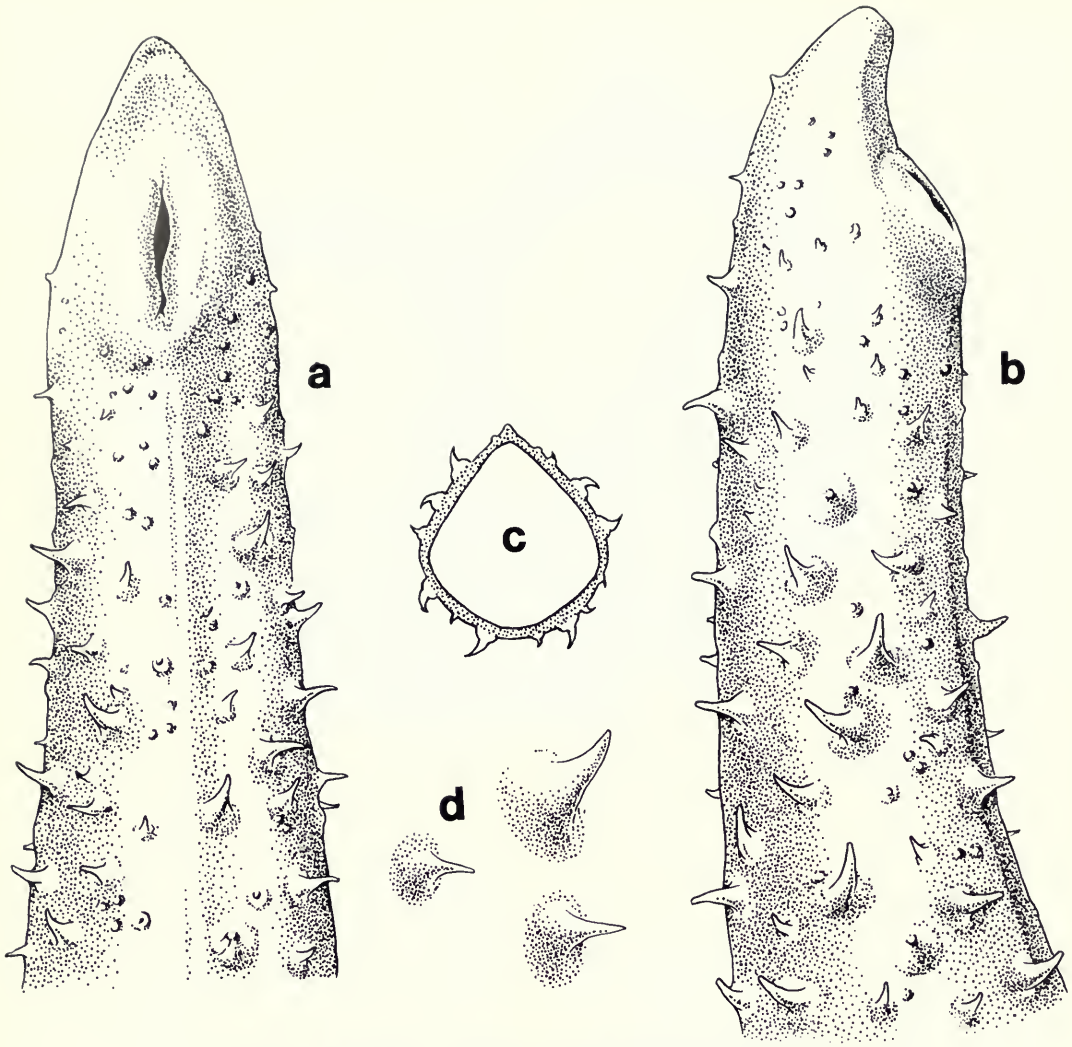


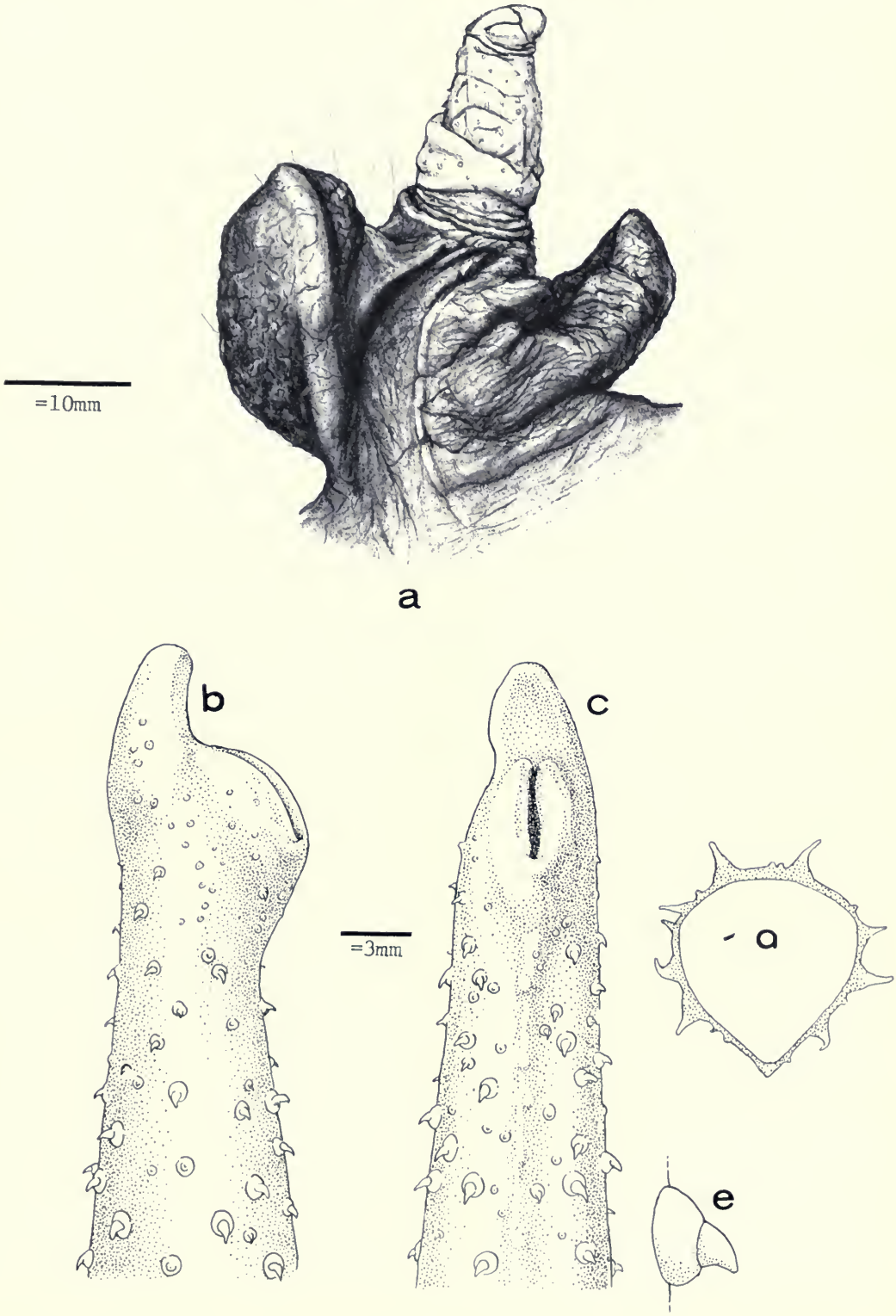
FIG. 5. *Cacajao melanocephalus* (FMNH 78567; KOH preparation); **a,** ventral surface of shaft; **b,** same, right side; **c,** same, cross section (apex dorsal); **d,** same, spines enlarged.

FMNH **60292 (no data) (fig. 6a)**—Scrotum ovate, entirely pigmented, the testes withdrawn, greatest stretched transverse diameter about 55 mm, skin puckered and convoluted, thinly hirsute, nearly nude in appearance, covered with small glands opening to surface; perineum pigmented, the perianal portion with short spines; penis tapered, prepuce pigmented basally, unpigmented distally, shaft unpigmented, base to tip about 50 mm, diameter at base of prepuce about 10 mm, transverse width of glans 6 mm, length 8 or 9 mm; meatus 4 or 5 mm, lateral borders swollen, the ventral with swollen lappet about 4 mm transversally; penis including prepuce and glans studded with large grap-

→

FIG. 6. *Cacajao calvus,* external genitalia of mature male; **a,** intact, anteroventral aspect, testicles retracted, right sac partially stuffed with cotton, left sac relaxed (FMNH 60292); **b,** distal portion of shaft, right side (MPEG 8990, KOH preparation); **c,** same, ventral aspect; **d,** same, cross section of shaft, narrow side (apex), ventral; **e,** same, spines enlarged; the several directions of spines appear to be natural but may be artifacts of preparation and preservation. Sample figured is the only one available.

CACAJAO CALVUS



pling spines each with expanded base; longitudinal axis of staff slightly concave dorsally, moderately convex ventrally, subtriangular in cross section, the apex ventral, cant right, the shaft twisted about 30° to right of scrotal raphe; baculum not palpable.

MPEG 8990 (juv.) (figs. 6b-e)—Length of cleared penile fragment with tapered shaft 23 mm, diameter at base 10 mm, distally behind meatus, 5 mm; shaft with longitudinal axis of dorsal surface slightly convex, crested, ventral surface concave, staff subtriangular in cross section, apex ventral, cant right; prominent spines recurved, each rising from swollen base; meatus bordered by swollen lips on sides, lappet below protruded; baculum absent.

Cacajao calvus rubicundus I. Geoffroy and Deville

RNHMS 630142 (GSL = 102.1)—Cleared penile fragment about 25 mm long, shaft with dorsal curvature plane, ventral convex, cross section subtriangular, apex ventral, cant right; spines and glans as in preceding; baculum absent.

Hill (1958, p. 645, 1960, p. 227, figs. 48, 49)—The 1958 description of the genitalia of an unnamed species could apply to adults of either or neither of the two species of *Cacajao* but more likely to either an immature *Cacajao calvus rubicundus* or *C. c. ucayalii*. The crudely figured glans appears asymmetrical but it may be the lateral aspect that is shown.

The detailed description of developing and mature genitalia of *Cacajao calvus ucayalii* observed by Fontaine and Du Mond (1977, pp. 201, 203) in the seminatural environment of The Monkey Jungle, in Goulds, Florida, follows.

> Examination of the external genitalia of *Cacajao* allows easy sexual identification of adults while providing uncertain clues as to the sexual identity of younger animals. The most probable basis for this condition is the occurrence in the male of a developmental stage of several years duration in which the external genitalia and other characteristics of the male approach the adult female in form. Female red ouakaris lack this developmental stage which begins in the male's fourth year. Their development proceeds directly from the juvenile condition to adulthood in the fourth year. Thus, the external genitalia of infants and juveniles appear similar in both sexes because these young ouakaris are in the process of developing the apparently similar external genitalia of adult females and subadult males.
>
> In the adult male the testes are fully descended. The scrotum is a black pendulous[!], flaccid, asymmetrical bilobed sac. . . . It is entirely hairless[!] as described by Kinzey (1971).
>
> The penis of the adult male appears large in proportion to other perineal structures. The prepuce encloses the proximal half of the body while tiny spicules cover the exposed distal portion of the body. The glans is poorly differentiated from the body and, as mentioned by Hill (1960), the penis is laterally compressed along its length. With the exception of a ring of black pigmentation around the external urethral meatus, the distal portion of the penis is entirely unpigmented.
>
> The external genitalia of the subadult male red ouakari presents a marked contrast with the adult male condition. The subadult male scrotum consists of a pair of rugose, black, hairless, symmetrical, parapenial scrotal alae that superficially resemble the adult female labia. Roughly triangular, and broadly attached to the pubic region, each pendulous scrotal lobe is distinct from its opposite member, but connected by a bridge of apparently similar tissue postpenially. The testes appear undescended at this level of development. The prepuce covers the entire length of the subadult's glans penis which only becomes visible during erection.
>
> Hill (1960) provides a detailed account of the external genitalia of *C. rubicundus ucayali* [= *C. c. rubicundus*]. In comparison with males observed in the "Rainforest," his description conforms to a transitional stage between the adult and the subadult.
>
> The sexual identification of juvenile and infant ouakaris on the basis of field characteristics is problematical. Male and female external genitalia do not have obvious differentiating characteristics during the first two years of life. . . . In these animals, the external genitalia consist of three hillocks in the pubic region that are more darkly pigmented than the surrounding regions. During vigorous locomotor play in the male, erection of the penis occurs allowing the unpigmented penis to protrude beyond the preputal [*sic*] anlage. The absence of visible erection characterizes the young female.
>
> The external genitalia of the adult female

resemble those of the subadult male. The glans clitoridis and preputium clitoridis of adult females in the seminatural environment form a dusky hillock anterior to the rima pudendi. To each side of the rima pudendi lie black, rugose, pendulous labia. These structures superficially resemble the scrotum of the subadult male; however, their relatively uniform lateral thickness, their relatively gracile character, and their tendency to form an acute angle anteriorly allow discrimination of the adult female labia and the subadult male scrotum. A constriction of the labia about halfway along their ventral extent which may correspond to a demarcation between the labia minora and the labia majora provides another characteristic facilitating the identification of adult females.

Hill's description of the female genitalia of a specimen of *C. rubicundus* [= *C. c. ucayalii*] probably represents a female about 3 years of age that was in the process of acquiring adult characteristics. The pendulous character of the labia was not developed in this specimen. Hill's (1960) account suggests that the pendulous labia of the adult female ouakari may represent fusion of the labia minora and the labia majora with the portion homologous with the labia majora extending most ventrally.

Morphology and Phylogeny

Baculum

Pitheciine bacula are in the process of disappearing in the wake of differentiation of an ostensibly unique system of sperm delivery within the group. The baculum has been lost in *Cacajao* and *Chiropotes* except for scattered vestiges of disintegrated embryonic bacula detectable in the cleared and stained glandes of a few adult specimens (table 1).

The baculum in *Pithecia* is dorsomedian, the urinary meatus ventromedian directly behind the anteromedian lappet. The lobes on each side of the opening are symmetrical. Hershkovitz (1977, p. 119) observed that the meatus of the Callitrichidae, Callimiconidae, most cebids, nearly all cercopithecids, and some anthropoids is skewed to the right with the left lobe of the glans containing the baculum larger than the right. The asymmetry persists in atelines and *Aotus* with baculum lost or vestigial. An *Aotus* [sp.?] in the British Museum (Natural History) with baculum 2.2 mm long was reported by Dixson (1987a, p. 52).

Evidently, loss of baculum in the symmetrical glans of pitheciines, *Homo*, *Tarsius*, and the asymmetrical glans of atelines and *Aotus*, are parallelisms.

Correlations between baculum length and body weight in 74 adult primates representing 46 species were described as positive by Dixson (1987a). The length of the baculum also appeared to be correlated with copulatory behavior in 34 species for which detailed information was available. The study animals included *Pithecia albicans*, with baculum length 1.5 mm and copulatory behavior and weight unknown. The small baculum, however, does correlate with small body size as determined by Dixson (1987a, table on p. 53). The same is true of other individuals of *Pithecia* with baculum intact. All other pitheciine genera are much larger and lack bacula. In their case, Dixson's correlations do not apply.

Penile Shaft

Pitheciine penes have departed from the hypothetical ancestral, subcylindriform organ to a small, tapered, bluntly pointed glans, the shaft with dorsal longitudinal axis either convex (penis pointed down or distally) or concave (penis pointed up or proximally), sides compressed, the organ in cross section subtriangular with apex dorsal or ventral, the shaft curved or canted to left or right.

Penile cant in *Pithecia monachus*, as in *Cacajao calvus*, is to the right; that of the remaining pitheciines is to the left except in *Chiropotes satanas* where it may be right or left. The single cleared mature penis available of *Chiropotes albinasus* resembles those of *Chiropotes satanas* except possibly by its dorsal longitudinal convexity. The penis of *Cacajao calvus* differs primarily from all others by the narrow or apical aspect of its ventral surface (table 2). More samples of each species may reveal variation not apparent in the single or few available samples.

Observations—In his study of primate genitalia and behavior, Dixson (1987b, p. 439) noted that penile morphology and copulatory patterns "tend to be more specialized in species which have a multimale or dispersed (non-gregarious) mating system. The penis may be longer and more complex morphologically in such species." Among the

130 species Dixson examined, the pitheciine *Cacajao calvus* (two specimens) was listed among the multimale societies, its penis indicated as moderately complex. Attribution of a baculum to the species, however, may be questioned. Included among primates with a monogamous mating system were the comparatively unspecialized *Pithecia pithecia* and *P. albicans.*

Present data indicate that correlations drawn by Dixson between baculum, penile complexity, spines, body size, and copulatory behavior could be the same with or without the baculum.

Scrotum

All pitheciine scrota are sessile and parapenial, ovate in *Cacajao* and *Chiropotes,* pear-shaped in *Pithecia*; skin in preserved condition puckered in parts, sulcate, convoluted or corrugated in others, the sebaceous glands showing as pitted welts, the long pigmented hairs arranged in triads each emerging from a pore; a short hair flanks each side of each triad.

The eight available scrota of *Chiropotes satanas* are mostly asymmetrical without evident polarity. In *Pithecia,* the pigmented perineum is hairy, the raphe extending nearly to proximal border of glans; in *Chiropotes,* the bare, pigmented raphe continues well defined to the scrotal base and continues almost imperceptibly to base of prepuce. The pigmented perineum is beset with short, thick spines.

Spines

The conical recurved spines are formed of overlapping scales of keratinized epidermis. Worn, broken, or cast-off spines are renewed as evidenced by spines of all sizes and in all formative stages.

Spines of monogamous *Pithecia* are minuscule, each with a nodular base and altogether too small for effective hooking or grappling. They may, however, provide stimulation during intercourse. Spines of so-called multimale groups *Chiropotes* and *Cacajao* are large and hooked. Those of *Cacajao* attain a length of nearly 1.0 mm. Those of the tumescent penis of both genera can be erected, possibly for heightened sensitivity during preintromittent probing. During intromittent thrusting, spines may assist in the disintegration of vaginal plugs formed from prior multimale ejaculates or may hook into the vaginal mucosa to form a lock. Penes of juvenals and subadults have no need to lock. They lack spines.

Effects of penile spines on the copulatory behavior in primates were tested by Dixson (1991) on the common, generally monogamous marmoset, *Callithrix jacchus.* Sixteen sexually experienced captive-born males and 10 females with similar histories were used. "The major effect of spine removal," Dixson (1991, p. 561) found, "is to increase the duration of pelvic thrusting required to attain intromission, with some effect also upon the duration of intravaginal pelvic thrusting. Spine removal has no effect upon penile erection or upon the ability of males to orientate correctly when mounting females. However, the ability to locate the vaginal orifice during bouts of rapid preintromission pelvic thrusts is impaired in these animals."

Sexual Behavior

The sexual life of pitheciines is little known. A monogamous social system of certain, if not all, species of *Pithecia* is inferred from field observations of paired or family group associations of *P. pithecia* (Buchanan et al., 1981) and *P. monachus* (Moynihan, 1976; Izawa, 1976). My field observations of both species confirm those reports. Information on the social system of remaining species (*P. irrorata, P. albicans,* and *P. aequatorialis*) is lacking. Observations of actual mating and copulation among free-living sakis have not been recorded.

The two species of *Chiropotes* (*C. albinasus* and *C. satanas*) associate in so-called multimale groups, actually composed of both sexes of all ages (Ayres, 1981). Again, nothing is known of sexual play and copulatory behavior of either species. Each of the two species of *Cacajao* also form "multimale groups," correctly, multimale–female or cosexual congregations. Sexual behavior of wild-living *Cacajao melanocephalus* has not been recorded. That of *C. calvus rubicundus* has been studied in the seminatural environment of The Monkey Jungle, Goulds, Florida, by Fontaine and Du Mond (1977, pp. 207–209). Their account follows.

> Observations of the sexual behavior of Cacajao at Monkey Jungle have been largely confined to sexual relationships between juvenile males and adult females. The adult male's involvement in defensive responses to human

intruders interferes with his conduct of sexual relations in the presence of observers. Enough observations of adult male sexual behavior have been collected, however, to allow description of the major elements of Cacajao's sexual behavior.

The adult female displays some postural variability during copulation. She may lie prone with all four limbs flexed under her body or she may allow her limbs to dangle freely beneath her. Less frequently, the female lowers her hindquarters and maintains them in flexion during copulation while raising the forequarters. During copulation, the male sits behind the female with the thighs abducted and flexed. In juvenile copulations, the males were observed to flex their hindlimbs at the knees allowing the feet to maintain a firm grip on the small of the female's back (Fig. 6). The latter aspect of juvenile copulation may have been overlooked in adult male copulation. However, since this feature of juvenile copulation serves to "lock" the male into a secure position of dorsal-ventral contact with the female, it may prove to be a typical aspect of copulation in Cacajao.

Copulation in *Cacajao* requires several minutes. The typical copulation consists of a series of intromissions each accompanied by multiple pelvic thrusts by the male partner occasionally aided by complementary movements by the female partner. Periods of withdrawal alternate with periods of intromission. During these withdrawal periods, behavior is quite variable, ranging from general body contact to rapid travel to another location to continue copulation. . . .

Postcoital behavior in the adult male usually includes smelling of the female genitalia followed by a bout of mutual social grooming. The juvenile male, in contrast, usually leaves the female after a few cursory genital sniffs.

Cacajao does not include patterns such as genital presenting, pelvic thrusting, etc. within its repertoire of non-sexual social signals. On the other hand, the ouakari's long mantled fur hinders the observation of intromission and ejaculation and the detection of copulation plugs.

The large mixed sex and age associations or troops of *Cacajao* or *Chiropotes* described by some (Ayres, 1981; Roosmalen et al., 1981) as consisting of up to 30 individual and more, and by others as from 100 to 200 (Olalla, 1955), suggest a mating pattern of sexual promiscuity.

Testis size, sperm quality and quantity, and sperm competition within and between multiple ejaculates have been discussed by Møller (1988). According to Gomendio and Roldan (1991), sperm length is longer in polyandrous species than in monogamous species and is positively correlated with maximum sperm velocity. Neither report mentions pitheciines with mating systems that encompass monogamy, polyandry, and penes with or without baculum. Neither considers the probability that among females hierarchical controls and physiological responses to sperm stimuli might enforce a degree of selectivity.

Conclusions

Evolution of pitheciine male genitalia has given rise to what could possibly be a unique system for direct sperm delivery into the uterus. The process involved reduction or elimination of the baculum, curvature of the shaft with lateral compression and taper to a small bluntly pointed labile glans, emergence of meatal erectile clasping bodies or lappets, and in *Chiropotes* and *Cacajao* hypertrophy of penile spines for clearing passage through the vagina and locking.

The penis such as that of *Pithecia* with a simple or nearly cylindrical form covered with minuscule spines could give rise to organs such as those of *Chiropotes* and *Cacajao*. The pigmented strongly tapered penis of *Cacajao* projects from near the inguinal border of the scrotum and curves upward with a sidewise twist of more than 30°. The longitudinally concave curvature of the unpigmented ventral surface of the *Chiropotes* penis is like that of *Cacajao*, but the narrow side or apex is dorsal, not ventral as in *Cacajao*, the member itself turned sidewise to as much as 45° against the scrotum. The boneless, curved pitheciine shaft simulates or equates with the long terminally curved or hooked baculum possessed by many kinds of mammals (cf. Burt, 1960).

In all cleared penes, the arrangement of the tumescent lappets surrounding the meatus take on the form of a gasket. In coitus, the glans likely penetrates to the level of the cervix. Conceivably, at that point the labile gasket-like meatus clamps onto the cervix and stimulates opening of the cervix for transfer of ejaculates into the uterus. In *Cacajao* and *Chiropotes*, the penis with its labile

glans is already curved and twisted upward toward the cervix. During coital convulsions, an extensile cervix might make the additional quarter turn to couple with the glans. Adhesion between cervix and meatus of a particular male most likely depends on selective responses of the female apparatus. Where meatus and cervix are normally not opposed as, presumably, in nearly all other primates, the described maneuver would not be possible. In a sperm delivery system, described by Fooden (1990, p. 631) for the bear macaque, *Macaca arctoides,* "the prominent vaginal collicle, short vagina, and long exocervix in *M. arctoides* are apparently morphologically complementary to the long, tapering glans penis in this species. . . . These complementary specializations of the glans and female tract appear reciprocally adapted to permit the glans to pass ventral to the vaginal collicle, through the short vagina, and into the long exocervix. Penetration of glans into cervix, as postulated here, has not been previously reported in catarrhine primates."

A baculum-stiffened glans as in perhaps 50% of *Pithecia* males might be less successful than the boneless glans in effecting embrace between meatus and cervix. Baculum or not, males of monogamous *Pithecia* are hardly if at all competitive with each other for insemination of the female. Spermatozoa of one saki, once delivered, presumably do not compete with those of other males as might be the case in multimale groups.

Among primates, seminal vesicles, of importance in the ejaculatory process, are reported absent in the monogamous *Pithecia* and *Callicebus* (by Harrison and Lewis, 1986, table, without reference to original sources) and in *Daubentonia* by Eckstein (1958, p. 554). In these genera, vaginal plugs would not be needed and may not be formed. According to Voss (1979), nearly all male rodents form vaginal plugs in the female vagina for chastity enforcement. Voss (1979, tables 3, 4) adds, however, that among the 24 murid species he examined, the three that are monogamous form no vaginal plugs. These species were further distinguished by highly modified or missing seminal vesicles and presence of a complete copulatory locking system. The locking system, according to Dewsbury (1972), has not been observed in primates. It seems, rather, that it may exist at least among pitheciines (cf. p. 14), and some callitrichids (Hershkovitz, 1977, p. 418).

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